

The ultrastructure of leg skin in the phylogeny of spiders

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The ultrastructure of leg skin in the phylogeny of spiders. - The ultrastructure of the leg skin was studied with SEM in most spider families. The plesiomorphic leg skin type in labidognath spiders is ridged and is also predominant in most Amaurobiomorpha (RTA Clade + relatives). Ridged skin is correlated with the presence of several types of hairs, longitudinally ridged bothrial base, and in the majority of families (RTA Clade) also by the presence of tarsal trichobothria. Araneoidea s.lat. (= Araneomorpha *sensu* LEHTINEN 1978) is characterized by scaly skin correlated with a single, serrate type of leg hair, smooth bothrial base, and lack of tarsal trichobothria. Both skin types may be secondarily modified, but there are no known cases of reversal to the ridged type in Araneoidea s.lat. Scaly or ridged scaly types not homologous with the Araneoidean type have evolved in parallel in some groups not related to each other, but the phylogenetic position of the groups outside Araneoidea s.lat. is demonstrated by the presence of other, correlated synapomorphies of Amaurobiomorpha and some other groups (Mecysmaucheniidae, Drymusidae, Caponiidae). Some subfamilies or still unnamed infrafamilial groups in Zodariidae, Corinnidae, Caponiidae and Palpimanidae have modified leg skin, in spite of presence of ridged skin in other groups of the same family. Nicodaminae with scaly skin and Megadictyninae with smooth skin are probably not closely related. Papular skin is dominant in Thomisidae, but smooth in Nesticidae. Ultrastructural results in Uloboridae, Mimetidae, and Archaeoidea support some alternatives in the phylogenetic placement of these groups with disputed relationships. The evolution of the Mygalomorph skin type, as well as the the outgroups of the main subdivisions of the order Araneae remain unresolved.

Key-words: leg skin - ridged type - scaly type - ultrastructure - SEM.

INTRODUCTION

Phylogenetic analyses for the main groups of spiders have recently been carried out using computer programs with little or no methodological checking. The computer has been very effective in the time-consuming comparison of complex

matrices, and most of the results are obviously correct. However, a number of problems can be seen to arise, when this method is used without sufficient critics. Some merely technical problems of cladistic analysis have been discussed in detail, e.g., the missing characters by PLATNICK *et al.* (1991 *b*) and comparison of the advantages and disadvantages of the most common programs (PLATNICK 1987, 1988). As emphasized by PLATNICK (1989 *b*: 21): "The open question, then, is not so much how best to analyze a data matrix, but how best to represent organismic variation in the matrix". More precisely, incorrect results appear to be mainly due to misinterpretations of homologies and polarities, erroneous coding and deficiencies or unbalanced selection of characters.

If a majority of characters analyzed are associated with a single adaptation, a restricted complex of morphological and ethological characters, it is always theoretically possible to create a cladogram, where all taxa sharing this adaptation become "more related to each other than to other groups", independent of possible parallelisms in this adaptation. Accordingly, such an approach may omit or underrepresent characters of other, adaptively independent character complexes which may unite or separate taxa in entirely different ways.

The value of non-reversible single characters, e.g., the number of tarsal claws, is easily lost among the multitude of small reversible characters (details of genital structures) in computer programmes based on the principle of the most parsimonious tree. GRISWOLD (1993) used this principle without character weighting for the number of the tarsal claws and presented a cladogram of his "Lycosoidea" with numerous three-clawed groups "evolved" from two-clawed ancestors.

The ultrastructure of all chitinous surfaces includes a very large group of characters, the use of which has been quite restricted in most recent computer analyses of spiders. The leg skin of all labidognath spiders (= Araneomorpha s.lat.) is relatively monotonous, and only two basic types are present: ridged (Figs 1-2, 5-10) and scaly (Figs. 3-4, etc.). Some adaptive modifications are present in various families, mostly in spiders of dry habitats, but one of these two basic types is usually preserved in at least some details.

However, many of these characters are not correlated with other character groups or with behavioral adaptations, e.g., the numerous characters of the spinning organs that have predominated in most of these analyses.

The type of leg skin is very strongly correlated to the type and structure of unmodified hairs. The significance of these characters in spider phylogeny has been discussed by LEHTINEN (1967, 1971, 1975 *a, b*, 1976, 1978) and in Mygalomorphae by RAVEN (1985). A more reliable interpretation of modified leg skin types is made easier when other ultrastructural characters are analyzed together with those of the leg skin.

SEM micrographs of the leg skin of various spider families have often been unintentionally published in connection with depicted details of various leg structures, mostly the bothrial base or tarsal organ. Previous reports by this author (LEHTINEN & SAARISTO 1980, LEHTINEN 1981) have also included such data in written descriptions, but no interfamilial comparison was made. Useful SEM micrographs with or without

discussion of the findings have been published especially by Platnick's group working for AMNH: PLATNICK (1975, 1984 *a,b*, 1986, 1989 *a*, 1991, 1994 *a,b*), PLATNICK & LAU (1975), PLATNICK & GERTSCH (1976), GERTSCH & PLATNICK (1979, 1980), RAVEN & PLATNICK (1981), FORSTER & PLATNICK (1984), COYLE (1984), PLATNICK & GOLOBOFF (1985), FORSTER *et al.* (1987, 1990), GRISWOLD (1987, 1990, 1993), PLATNICK & FORSTER (1989, 1993), JOCQUE (1991, 1994), PLATNICK & GRIFFIN (1990), PLATNICK *et al.* (1991 *a*), PLATNICK & DI FRANCO (1992), PLATNICK & BRESCHOVIT (1994), and OVTHSHARENKO *et al.* (1994). However, wide-scale phylogenetic discussions based on this character are rare. The tarsal organ and the base of the bothria have been separately depicted in numerous recent papers, though no author has yet attempted to make a phylogenetic analysis based on such a widely studied character. Furthermore, no author has even sought to include a sufficient number of ultrastructural characters for computer analysis, nor have these two skin types or their modifications been correctly coded (CODDINGTON *et al.* 1991).

In contrast, some ultrastructural characters with a narrow range in spiders have been analyzed in detail, e.g., the tibial glands of the Leptonetids by PLATNICK (1986) and specializations of the tarsal organ of Microstigmatidae by PLATNICK & FORSTER (1982). The ultrastructural characters of the carapace, chelicerae, and abdomen were widely discussed by LEHTINEN (1981) in Tetrablemmidae and many of them have been sporadically depicted in SEM micrographs by other authors without their use for wide-scale phylogenetic analysis of higher taxa.

The present report concentrates to the results of a screening of the leg skin ultrastructure of most spider families with the aid of SEM-micrographs. The polarity of evolution of this and some other ultrastructural characters is discussed, as well as the meaning of these results for the placement of several groups with disputed relationships.

MATERIAL

For the present synthesis, the ultrastructure of the leg skin was compared between most spider families, mostly based on the author's SEM-studies, with reference made in some cases to reliable published data (for details, cf. introduction). More than 600 SEM micrographs of the leg skin were taken in 1971-1995.

The term "ridged" has been previously used by CODDINGTON (1990). The basic type characterizing this pattern consists of parallel ridges separated by furrows and could as well be called "furrowed".

For problematic families, especially Mimetidae, Uloboridae, Deinopidae, Palpimanidae, Zodariidae, and Corinnidae, the types of leg hairs and setae, bothrial bases, onychial structures, tarsal organ and other sensory organs (when present) were also analyzed in detail.

RESULTS

A. Leg skin type of different spider families/genera

The dominance of the unmodified ridged type has been confirmed in the following families:

Mygalomorpha: Dipluridae (*Allothele*), Nemesiidae: Diplothelopsinae (*Mygaloides*), Barychelidae (*Encyocrypta*) (Fig. 6).

Primitive Cribellata: Austrochilidae (Fig. 5), Hypochilidae, Gradungulidae (Fig. 7).

Haplogynae: Dysderoidea: Oonopidae s.lat., Orsolobidae, Segestriidae: Segestriinae; Scytodoidea: Ochyroceratidae, Telemidae, Leptonetidae; other haplogynae: Pholcidae, Caponiidae: Nopinae & Caponiinae (isolated family).

Palpimanoidea: Palpimanidae: Otiiothopinae (Fig. 8).

Amaurobiomorpha: separate cribellate groups: Psecridae (Fig. 2); Dinopoidea: Dinopidae (Fig. 44), Uloboridae (Figs. 1, 41-43); Oecobioidea: Urocteidae, Hersiliidae (Fig. 11); Lycosoidea: Lycosidae, Ctenidae, Cycloctenidae (Fig. 36), Dolomedidae, Zoropsidae, Trechaleidae; unplaced: Tenggellidae, Toxopinae, Miturginae (Figs. 10,34), Machadoniinae, Uliodoninae; Titanoecidae, Amaurobioidea: Amaurobiidae, Agelenidae, Anyphaenidae, Liocranidae, Zoridae (Fig. 9); Dictynoidea: Dictynidae, Hahnidae (Fig. 35), Desidae, Anyphaenidae; Pisaroidea: Pisauridae, Oxyopidae, Senoculidae; Clubionidae: Clubionidae, Micrommatidae, Heteropodidae, Philodromidae, Trachelidae; Salticoidea: Salticidae (Fig. 12).

Ridged type with predominance of a smooth or anastomosing type:

Haplogynae: Scytodoidea: Scytodidae; unplaced haplogynae: Pholcidae, Diguettidae, Plectreuridae, Tetrablemmidae; Eresidae (Fig. 21) Amaurobiomorpha: Palpimanoidea: Palpimanidae, Stenochilidae; Gnaphosidae: Gnaphosidae: Platorinae, Cithaeronidae, Prodidomidae, Trochanteriidae, Ammoxenidae; Zodarioidea: Zodariidae: Zodariinae (Fig. 19), Storenomorphinae, & Storeninae: *Cybaeodanus* & *Leprolochus* (Figs. 15,33), Cryptothelidae; Corinnoidea: Corinnidae: Corinninae (Fig. 20), Castianeirinae + several unplaced, ? family: Phrurolithinae.

Dominance of papular or smooth type:

Filistatidae (Fig. 18), Thomisoidea: Thomisidae: Thomisinae (Figs. 13,14.), Stephanopisinae, Stiphropinae, Homalonychidae (Fig. 22); Palpimanidae: *Palpiuanus*; Megadictynidae (Fig. 46).

Scaly type and absence of ridged type has been checked in all families of Araneomorpha s.str.:

Araneoidea: Araneidae (Figs. 3,40), Metidae, Tetragnathidae, Anapidae, Symphytognathidae, Theridiosomatidae, Mysmenidae, Linyphiidae, Mynoglenidae, Erigonidae, Mimeidae (Figs. 37,39), Micropholcommatidae (Fig. 38), Theridioidea: Theridiidae, Hadrotarsidae, Synotaxidae, two new groups of possible family status, Archaeoidea: Archaeidae, Holarchaeidae.

Finely granular/smooth type:

Nesticidae (Fig. 17), Cyatholipidae.

The presence of various "scaly types" in combination with remnants of the ridged type or hair bases and hair types typical of Amaurobiomorpha:

Gnaphosidae: Cithaeronidae (in some areas); Zodarioidea: Storeninae, Corinnidae (*Oedignathia*), Homalonychidae (Fig. 22), Nicodamoidea: Nicodamidae (Fig. 45).

Mygalomorph "scaly types":

Antrodiaetidae, Atypidae, Migidae, Ctenizidae, Idiopidae, Nemesiidae: Anaminae (*Anaue*) (Fig. 32), Hexathelidae (Fig. 4), Paratropididae, Mecicobothriidae, Microstigmatidae.

Autapomorphic "scaly-papular" types (not related to each other):

Heptathelidae, Liphistiidae (Fig. 31), Microstigmatidae (*Ministigmata*), Microstigmatidae: Micromygalinae (*Micromygalae*).

Mixed types (ridged scales):

Drymusidae (Fig. 24), Caponiidae n. subfam. (Fig. 26), Mecysmaucheniidae (Fig. 25), Corinnidae (*Sphingius*) (Fig. 23).

The type of leg surface is one of the most reliable characters in the phylogenetic classification of labidognath spiders, although many recent analyses (RAVEN 1985; CODDINGTON 1990) have treated this character as only a single character among various main groups of characters.

B. Outgroups

1) The generally accepted outgroup for the whole order Araneae is Amblypygi. The leg skin type of Amblypygi is scaly (PLATNICK & GERTSCH 1976; personal studies), but a review of the other Arachnid orders reveals that this could be an autapomorphy for Amblypygi within the branch Amblypygi + Araneae.

The leg skin structure of the other orders is quite variable (Figs 27-30), with all main types of spider skin also being present in other groups of Arachnida. Frequently, two entirely different types of leg skin are present in the metatarsi and tarsi of a single specimen, as in the opilionids of Stylocellidae (Fig. 30) and Phalangodidae. The scaly leg skin type is common to anactinotrichid mites (Fig. 29) and the ridged type to actinotrichid mites (Fig. 28).

2) There are several alternative outgroups for different suborders of spiders. However, these problems cannot be ultimately resolved by the results of this study.

Liphistiomorpha and Mygalomorpha.

The leg skin structure has been preliminarily studied in various mygalomorph and in both liphistiomorph families. The leg skin structure of Liphistiomorpha (Fig. 31, cf. also PLATNICK & GOLOBOFF 1985) could be classified as scaly, but it is unique among Araneae. Moreover, many of the other ultrastructural characters (structure of the bothrial base and tarsal organ) differ from those of all known labidognath spiders. The heptathelid "scales" are separate, rounded triangular extensions of the skin, well separated by continuous, nearly smooth skin. It is difficult to derive this type from the basic scaly type of Amblypygi, nor do any of the mygalomorph groups seem to share this autapomorphy of the recent Liphistiomorpha.

The leg skin of mygalomorph spiders is much more variable than that of labidognath spiders. The presence of the ridged type has been confirmed in three seemingly unrelated genera (cf. results in p. 3). Various papular surfaces (Fig. 32) as well as nearly smooth surfaces may constitute modifications of the ridged type, but occasionally also of the scaly type (RAVEN & PLATNICK 1981).

Araneomorpha s.lat. (Labidognatha auct.).

Liphistiomorpha and Mygalomorpha together, or Mygalomorpha alone, have usually been suggested as the outgroup for other spiders. However, there are no ultrastructural characters that could directly confirm either of these alternatives. Since PLATNICK's (1977) first phylogenetic analysis of the main spider groups, Hypochilidae, Gradungulidae, and Austrochilidae together have been regarded as the outgroup for other Araneomorpha s.lat. (= Araneoclada).

C. Polarity of evolution

Attempts to use leg skin characters for phylogenetic analysis of the main groups of spiders have failed due to incorrect coding. For example, CODDINGTON (1990: fig. 2 & 3) added character 13/24 to previous matrices (FORSTER *et al.* 1987) as a new hypothesis and coded smooth cuticle plesiomorphic and ridged cuticle as synapomorphy for Gradungulidae, Austrochilidae and Araneoclada. Similarly, RAVEN (1985) coded smooth cuticle as plesiomorphic in some Mygalomorph groups.

Attempts to use bothrial base (CODDINGTON 1990: characters 6,7) have been even more unsuccessful, as the coding is not interpretable and such a "plesiomorphic entire base" claimed for bothria in Araneoclada has never been found by this author outside Araneomorpha s.str. among the hundreds of genera studied.

CODDINGTON (1990: fig 108, ch 49) coded the hair type of all Deinopoidea as "pseudoserrate" and placed this type as an intermediate type between the plesiomorphic plumose and apomorphic serrate (Araneoidea). A study of all possible ultrastructural characters in Uloboridae and many of those in Deinopidae has revealed no differences between the hair structures of Amaurobioidea, Dictynoidea, and Deinopoidea.

The plesiomorphic type of labidognath leg skin is ridged and is also shared by the outgroup Gradungulidae + Austrochilidae. This skin type is present both in the majority of the haplogyne and primitive cribellate groups, as well as in practically all groups of Amaurobiomorpha *sensu* LEHTINEN 1978. The exceptions include some Zodarioidea, Thomisoidea and Nicodamoidea that are here classified as modified branches of Amaurobiomorpha. The surface structure of tarsal claws is ridged in all spider groups studied, although dramatically reduced. The basal part of the tarsal claws often shows some "secondary hairs" (Fig. 33) confirming homology with the normal plumose hairs of Amaurobiomorpha and primitive cribellate group.

The smooth type of leg skin does not deserve much attention here, as it is always an autapomorphy of a restricted group and is correlated with adaptation to extreme environmental conditions. In most cases with predominantly smooth leg skin, the plesiomorphic pattern of this group can be found from restricted parts of the leg surface, often only in the structure of the bases of normal hairs. Virtually smooth legs have been found in *Atypus* (Atypidae), many haplogyne groups (Sicariidae, Digueidae, Tetrablemmidae), *Zodarion* (Zodariidae), *Rastellus* (Gnaphosoidea, Ammoxenidae), and *Nesticus* (Araneoidea, Nesticidae, Fig. 17). Published SEM micrographs show that the skin of some other Araneoidean group may be smooth, at least in some details depicted, as in Malkaridae: Sternodinae (PLATNICK & FORSTER 1987) and Cyatholipidae (GRISWOLD 1987). The smooth leg skin of *Brignoliella* (Tetrablemmidae, Tetrablemminae) is divided into parallel, tranverse fields, an autapomorphy that hardly represents a reduction of intervening ridges and furrows.

The density of the furrows varies greatly and reversals between the subtypes seem to be common. The densest furrowing has been recorded from Scytodoidea (Ochyroceratidae and Leptonetidae), while the unmodified furrows of Psechridae are among the most sparse. Frequently, there are thicker ridges separating fields of narrow ridges and furrows, as in *Tangaroa* (Uloboridae; Figs. 1,41-43). The regular ridges and furrows often tend to form more irregular, anastomosing patterns (Figs. 11,12). These autapomorphic patterns, while similar in appearance, certainly have evolved independently in Gnaphosoidea (cf. also PLATNICK 1984 *a, b*, 1991), Lycosoidea (PLATNICK & FORSTER 1993) and Corinnidae: Castianeirinae.

Mygalomorpha has not been sufficiently investigated for ultrastructural characters, but the presence of the ridged type in several mygalomorph lineages implies that the ridged type is even plesiomorphic for the whole order.

The polarity of evolution of some repeatedly discussed araneomorph (s.str.) characters must be emphasized here, when attempting a phylogenetic classification of all spider groups. The bothrial pattern of the haplogyne groups (not Caponiidae) and of all Araneomorpha *sensu* LEHTINEN 1978 has earlier been shown to be plesiomorphic (LEHTINEN 1980). The apomorphic patterns of Amaurobiomorpha have occasionally been secondarily reduced in regard to tarsal bothria, though a complete reversal to the plesiomorphic type is not known and can hardly be expected to occur. The plesiomorphic homologue of colulus in Araneomorpha *sensu* LEHTINEN is a long, unpaired, spinneret-like structure, while the corresponding plesiomorphic state of this structure in Amaurobiomorpha is the cribellum. No direct reversals are known for this structure, while the filistatid cribellum could represent homoplasy. The derivation of Araneomorpha s.str. (= Araneoidea auct.) within the RTA-clade in Amaurobiomorpha is impossible, and all further problems can be resolved by acceptance of the parallel evolution of the cheliceral peg teeth (Pholcidae, Palpimanoidea, scattered Araneomorpha s.str.) and the most effective type of web for prey catching, the orb web (Araneomorpha s.str. and Uloboridae).

DISCUSSION

The leg skin structure and related ultrastructural characters of normal and modified leg hairs are a very useful and also practical means for phylogenetic analysis of most suprageneric groups, including at least the main groups of labidognath spiders. The polarity of evolution in leg skin type and most other ultrastructural characters can be easily demonstrated, and the coding of characters is easy, with the exception of some modifications of the bothrial base which still need additional work.

For classification of most spider families, the results of this analysis simply confirm the results of other recent work on spider phylogeny. However, this analysis should provide support for resolving the classification of those groups for which there is strong disagreement. The leg skin structure of Uloboridae, Palpimanidae, Mimetidae, and Nicodamidae needs special discussion here, and for those families many other ultrastructural characters will also need to be summarized.

No reversals from the apomorphic scaly types back to the plesiomorphic ridged type are known and could hardly be expected. The scaly skin type most probably has evolved more than once during the evolution of the order Araneae, as it has certainly done within the class Arachnida. The scaly skin type of the large group Araneomorpha *sensu* Lehtinen is correlated with numerous character groups outside the ultrastructural characters. This group is therefore easily separated from other spider groups with primarily scaly skin and several, possibly autapomorphic subtypes (Liphistiomorpha, many Mygalomorpha, Zodariidae: Storenidae, Nicodamidae: Nicodaminae). These groups showed entirely different character states, when compared with the other characters of Araneomorpha s.str.

Mygalomorpha. RAVEN (1985) presented the first modern analysis of phylogenetic relationships of Mygalomorph families. Leg skin type was sometimes

included in his matrices (p. 26) as a single character, but unfortunately not in the comparison of all families, and when used, smooth skin was interpreted to be plesiomorphic. Such polarity most probably does not hold for any arachnid group.

The radiation in the evolution of the leg skin types of Microstigmatidae is exceptionally wide (cf. RAVEN & PLATNICK 1981; PLATNICK & FORSTER 1982). *Micro-mygale diblemma* has unique combination of scaly skin and longitudinal ridges on the bothrial base. These ridges are more widely spaced than in the known ridged patterns in other spider families, and this bothrial type is not considered to represent a reversal of evolution.

The limitation of many mygalomorph families by RAVEN (1985) and GOLOBOFF (1993) is quite different from previous efforts, with both two classifications also differing from each other. The results of the present study support some details of both, but a detailed discussion of the classification of this group is here omitted.

Araneomorpha *sensu* LEHTINEN 1978 (= Araneomorpha s.str.). The limitation of this group must be revised by classifying the Archaeoidea as a primitive sister group of Araneoidea s.lat. (= remaining Araneomorpha s.str.). Deinopidae and Uloboridae were originally excluded as well as all Palpimanoidea s.str. (all with ridged skin). The group diagnosis of Araneoidea s.lat. includes many convincing synapomorphies:

Scaly leg skin; simple bothrial base; only one, serrate type of leg hairs with insignificant modifications; male genital bulbus basically with complex embolic division and apicodorsal modifications of palpal tibia (when present); anterior median spinnerets evolved to an unpaired, elongate colulus, when preserved at all (cribellum never present); subglobular to high oval abdominal shape; and abdominal modifications present in several lines of evolution.

The plesiomorphic state is usually preserved in simple bothrial pattern (no tarsal, one metatarsal); prey caught with non-tubular web; and chelicerae armed with teeth on both margins.

Mimetidae shares all the studied ultrastructural characters with Araneoidea (Figs. 37,39) and its assignment to Palpimanoidea has previously been widely questioned. Finally PLATNICK & SHADAB (1993: 4) admitted that the cheliceral characters "are not ideal" and presented SEM micrographs of the aberrant subfamily Oarcinae, where both the scaly skin and bothrial base are similar to Araneoidea.

Exceptionally smooth skin has also evolved also within this main line of evolution (some Nesticidae), but this observation causes no problems in the phylogenetic assignment of this family.

Archaeoidea & Palpimanoidea. The bothrial base in Mecysmauchenidae and Archaeidae is more complex than in Araneoidea (several concentric ridges in the arched part). Other ultrastructural characters of chitinous parts (also leg skin types) afford transitional states between the ridged and scaly types, with the type of genital organs being more primitive than in any other "Araneoclada". Archaeidae and Mecysmaucheniidae (Fig. 25) were placed on top of the cladogram of Palpimanoidea (FORSTER & PLATNICK 1984), though all their leg skin characters are plesiomorphic,

when compared with Mimetidae and Micropholcommatidae (Figs 37-39). The results above suggest derivation of all Araneoidea s.lat. from Archaeoidea, but even then Uloboridae must be excluded and it cannot be placed together with other orb-weavers.

Palpimanoidea s.str. (= Palpimanidae *sensu* SIMON 1903, including Stenochilidae, and Huttoniidae) are probably primitive relatives of Amaurobiomorpha, although many of their characters are strongly modified due to adaptations. The original ridged type is found even in the most modified Palpimanidae (*Steriphopus* & *Palpimanus*), where some parts of the femur and most of the bases of normal hairs even in the more distal segments have these ridges, although most of the leg surface is smooth or irregularly modified (Fig. 16). A considerably more ridged form of leg skin has been preserved in the more plesiomorphic *Otiotrops* (Fig. 8), as well as in Stenochilidae (*Colopea*).

The polyphyly of Palpimanoidea *sensu* FORSTER & PLATNICK 1984 seems to have now been finally confirmed and the presence of cheliceral peg teeth, the main "synapomorphy" for that group, is found to be convergent in spiders. Palpimanidae and Stenochilidae share the Amaurobiomorph type of normal hair structure and the number of hair types. While, the most often studied ultrastructural character, the type of the bothrial base, is aberrant but not comparable with any of the bothrial base types present in the Araneomorpha s.str. with scaly skin.

Amaurobiomorpha *sensu* LEHTINEN 1978/RTA-clade *sensu* CODDINGTON & LEVI 1991. Amaurobioidea, Dictynoidea, Lycosoidea, Clubionoidea, Heteropodoidea, and Pisauroida all share the plesiomorphic leg skin type and many other plesiomorphic morphological characters. Gnaphosoidea and Salticoidea are generally more apomorphic, but are easily assigned to the main branch of Amaurobiomorpha. Zodarioidea, Corinnoidea, and Thomisoidea each have several autapomorphies but most probably do belong within this group.

Deinopoidea *sensu* CODDINGTON 1990 was originally and is still included in Amaurobiomorpha. Its possible derivation from Psecchridae/Titanoecidae has been reviewed by SHEAR (1994). All claimed synapomorphies for Deinopoidea and Araneoidea *sensu* CODDINGTON, 1990 (p. 33 fig. 3: 11-16; fig. 108: 44-46, 49, 64-65, 67-69, 73, 77-78, 81-82) are characters either wrongly coded (108: 49) or strictly connected to a single adaptation, i.e., the use of orb web or its derivatives, with most of these (3:11-16; 108: 64-82) not being structural but ethological. The type of leg skin (Figs. 1, 41-43), the presence of many different types of leg hairs (including even feathery hairs: Fig. 44), the type of bothrial base and tarsal organ (Figs. 42-43), the sexual dimorphism of leg spinulation, and the presence of cribellum are all typical Amaurobiomorph characters. However, the details of the genital organs of Deinopoidea cannot be homologized with Araneomorph genitalia.

The leg skin structure of Amaurobiomorpha and the primitive outgroups (Hypochilidae, Gradungulidae and Austrochilidae) as well as all true labidognath haplogyne groups (Dysderoidea, Scytodoidea, and Caponiidae) is either ridged or secondarily smooth, while the longitudinally ridged bothrial base is dominant throughout these lines of evolution, strongly suggesting the plesiomorphic state of the ridged skin and longitudinally ridged bothrial base in labidognath spiders.

The anterior median spinnerets are represented by a bipartite cribellum that may lose its central septum, when reduced to a "pseudocolulus" (nonfunctional cribellum), this intermediate structure is always flat, not conical or fingerlike as a true colulus.

The most important synapomorphies for Amaurobiomorpha are: abdominal colour pattern with anterocentral folium; complex bothrial pattern (several metatarsal, a tarsal row with increasing length); numerous types of plumose hairs and sensory hairs; web with a basal tube, but often further modified or reduced (hunting habits).

Leg scopulae are never present in Araneomorpha s.str., but this is typically an adaptive character and possibly evolved several times within Amaurobiomorpha.

Distal bulbal as well as vulval and epigynal homologies between different main groups of spiders have been widely discussed and are very hard to prove. The genital structures of Amaurobiomorpha generally have many more similarities to each other than to those of any groups of Araneomorpha, but these characters are excluded here as strong evidence for any phylogenetic relationships. It must be noted here that genera with "palpal conformation" (cf. MILLIDGE 1977) of very different types and tegular processes ranging from none to four complex processes are sometimes found within a single family (Ochyroceratidae).

CODDINGTON & LEVI (1991:581) introduced the group "RTA Clade" which appears to be almost the same as Amaurobiomorpha. However, they excluded all groups that were insufficiently known (Cycloctenidae, Miturgidae, all Zodarioidea, Nicodamidae) as well as the "Lower Entelegynes" (Oecobiidae, Hersiliidae, and Eresidae), Palpimanidae s.lat. and Deinopoidea. RTA-Clade does not include any groups outside the original Amaurobiomorpha and could be called Amaurobiomorpha s.str. or sensu Coddington & Levi. The presence of a retrolateral tibial apophysis in the male palp is useful as such, but it has been reduced within the RTA Clade, at least in most Lycosidae, and shows parallel evolution in several groups of Araneomorpha s.str. Moreover, it is also present within the Eresid genus *Wajane*, as well as in problematic groups, placed by CODDINGTON & LEVI (1991) to "other" entelegynes.

Groups with disputable relationships

1) Thomisidae/Philodromidae. All Thomisidae have strongly modified leg skin (Figs. 13,14), at least partly papular. The leg skin of Philodromidae is ridged and similar to that of Heteropodidae. Feathery hairs are common to all Philodromids studied so far, but absent in Thomisidae, thus supporting the separation of Philodromidae from Thomisidae, originally based on other morphological characters (HOMANN 1975; DONDALE & REDNER 1976).

2) Corinnidae/Trachelidae/Liocraniidae/Phrurolithinae: Numerous genera of these groups have recently been transferred to other families (PENNIMAN 1985, PLATNICK & UBICK 1989, CODDINGTON & LEVI 1991, PLATNICK & DI FRANCO 1992, PLATNICK & BAPTISTA 1995). Several other genera were examined in this study with regard to several ultrastructural characters. Ultrastructural characters are quite useful for the definition of these amaurobiomorph groups, but most details will not be further discussed here.

Corinnidae usually shows a strongly modified type of leg skin with numerous modifications also in other ultrastructural characters (Figs. 20,23). However, the ridged type has been preserved in some details within most genera, *Supinna* being the best example. Phrurolithinae has similar, possibly parallel modifications, and both could be derived from somewhere within Amaurobiomorpha.

Both Liocraniidae and Trachelidae are characterized by the plesiomorphic type of ridged leg skin, with other ultrastructural characters being typical of Lycosoidea (Liocraniidae) or Clubionoidea (Trachelidae).

3) Zodariidae/Cryptothelidae: The leg skin tends to be strongly modified in Zodariinae (Fig. 19). The leg skin type of *Storena*, *Mallinella* and *Asceua*, at least, is scaly, although most probably not strictly homologous with other scaly types within Amaurobiomorpha. This is a convincing synapomorphy for this group of genera, though it is not shared by *Leprolochus* (cf. JOCQUE 1991). The type of leg skin found in Cryptothelidae supports the placement of this group as a sister group of Zodariidae sensu JOCQUE 1991.

4) Nicodamidae. The leg skin structure of Nicodamidae is best classified as scaly (Fig. 24). However, other ultrastructural characters, especially the presence of plumose hairs and, in general, the presence of several hair types on the legs, are not present in any Araneoidea. For these reasons, the "scaly" leg skin of this subfamily could be an autapomorphy. However, the suggested relationship of Megadictyninae to Nicodaminae (FORSTER 1970, HARVEY 1995) remains problematic, as the leg skin of *Megadictyna* is smooth (Fig. 18) and the evolution from Megadictynine cribellum to the conical colulus of Nicodaminae would be unique.

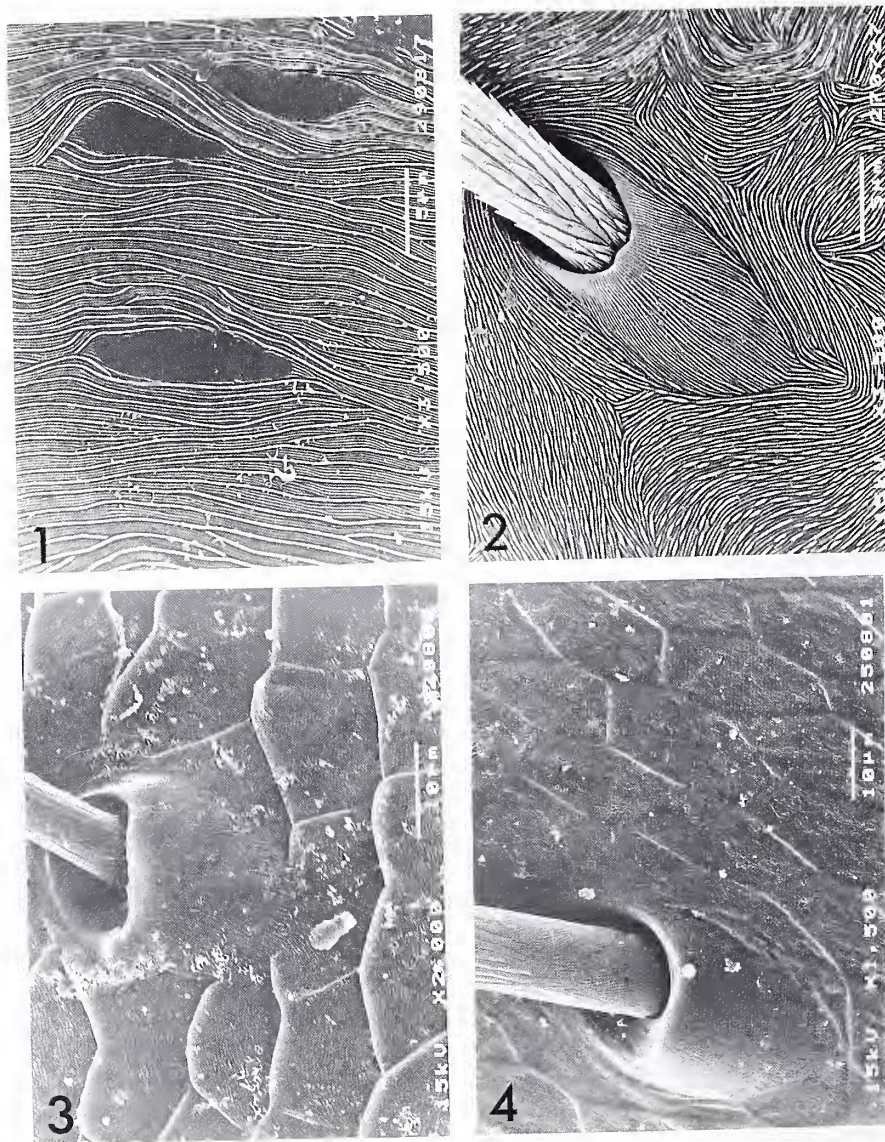
Ultrastructural characters in future cladistic analysis

This paper has mainly concentrated on the analysis of one important character of a very large character group and has focused on the consequences of previous misinterpretations of the polarity and variation of leg skin type. A cladistic analysis of all spider families/groups with an addition and correction of coding of ca. 15 other ultrastructural characters for leg morphology, as well as about 50-100 additional ultrastructural characters for mouth parts, carapace, abdomen, etc. will be the next necessary step to balance the matrices for a more comprehensive phylogenetic analysis of spider groups. At least, the easily coded characters should be added to the currently used family matrices with one strongly predominating character group (spinnerets and spinning activities). The other, sometimes very large group of characters, the genital organs, is plagued with problems of homology and therefore also with repeated problems of correct coding. Some other commonly used character groups, e.g., spine patterns and cheliceral armature have also shown repeated problems with correct coding. The classification of spiders today is very far from completion, especially with respect to the main groups of spiders above the family level.

ACKNOWLEDGMENTS

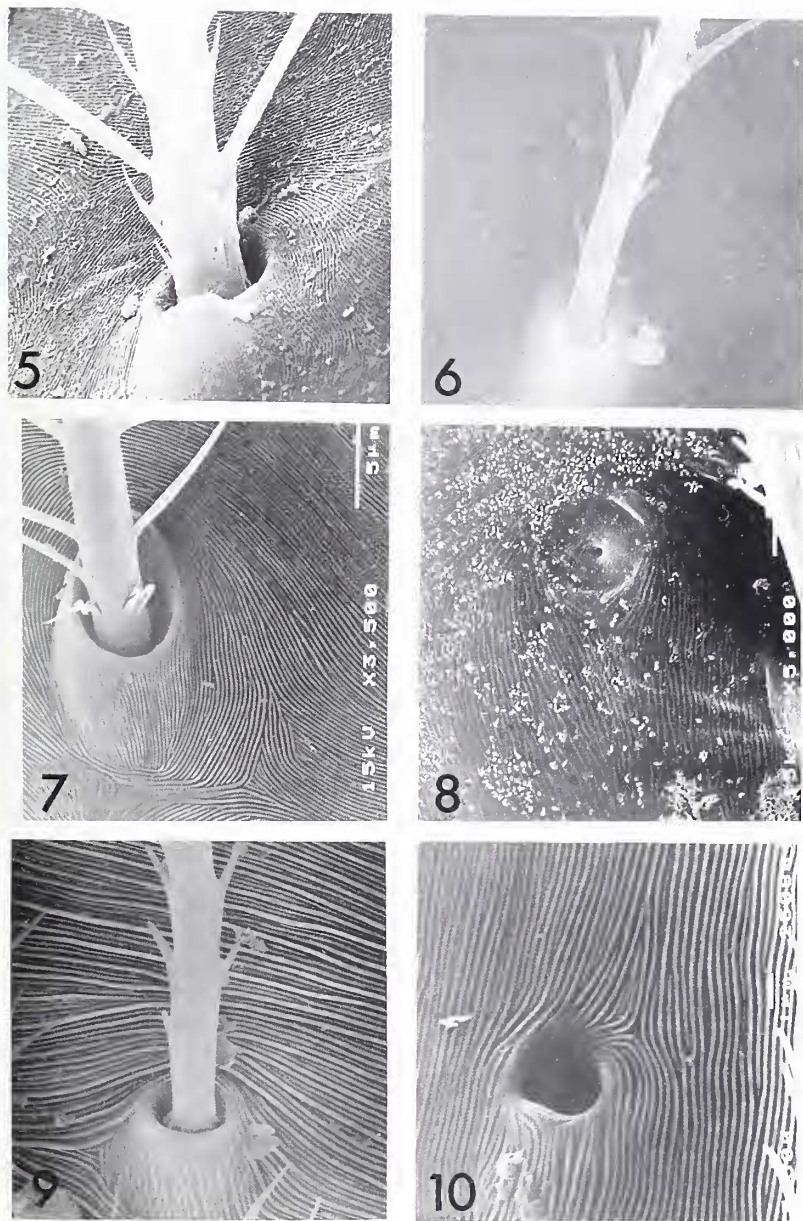
The editor and three referees made useful comments to the text of the lecture. Mr Ken Pennington kindly made the linguistic check.

The information about magnification in the SEM-micrographs concerns original magnification in 6 x 9 cm negatives. The exact final magnification can be calculated from the scale bar, when present. The suborder is Araneomorpha s.lat., when not otherwise indicated.



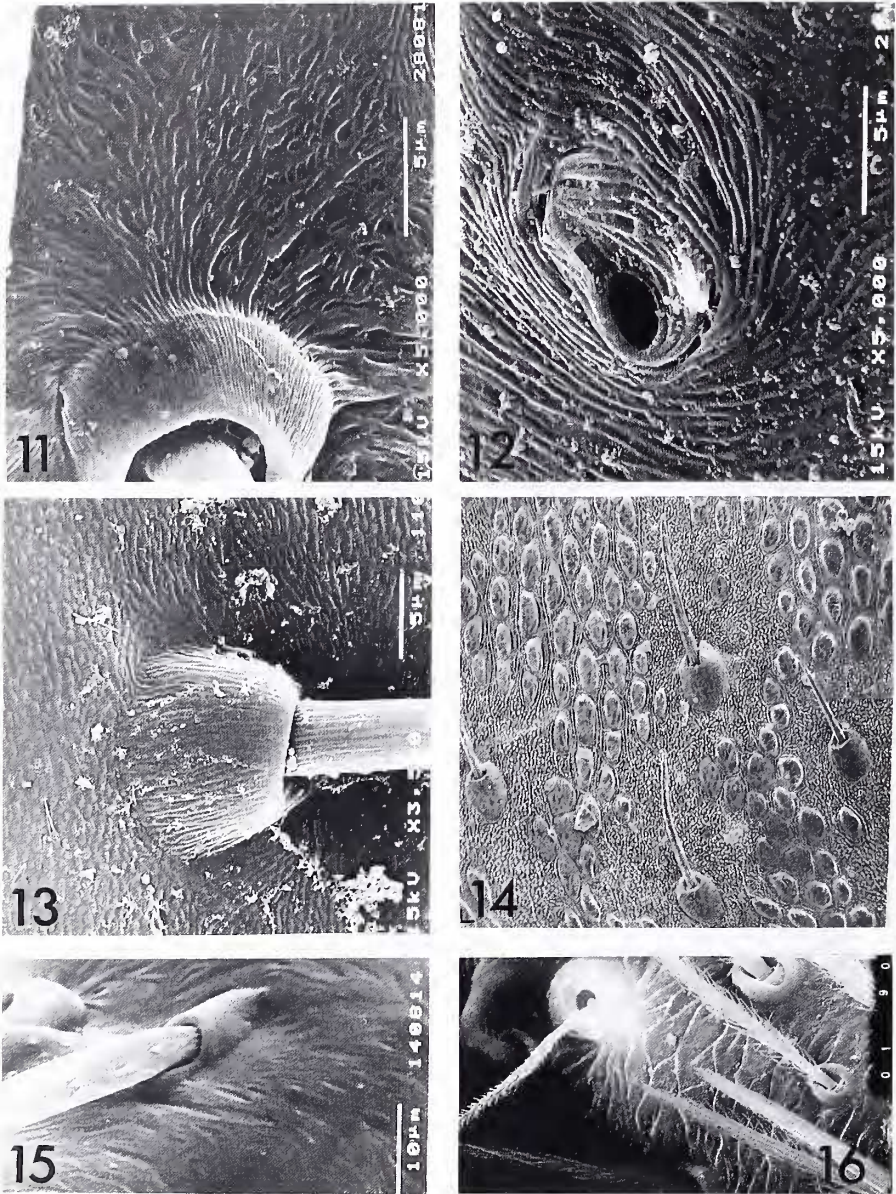
FIGS 1-4

Two basic types of leg skin in spiders: 1-2 ridged type, 3-4 scaly type. - 1: *Tangaroa tahitiensis* (Uloboridae), lateral field of palpal tibia; 2: *Psechrus argentatus* (Psechridae), tarsal surface; 3: *Araneus diadematus* (Araneidae), femoral surface; 4: *Hexathele montana* (Mygalomorpha: Hexathelidae), metatarsal surface.



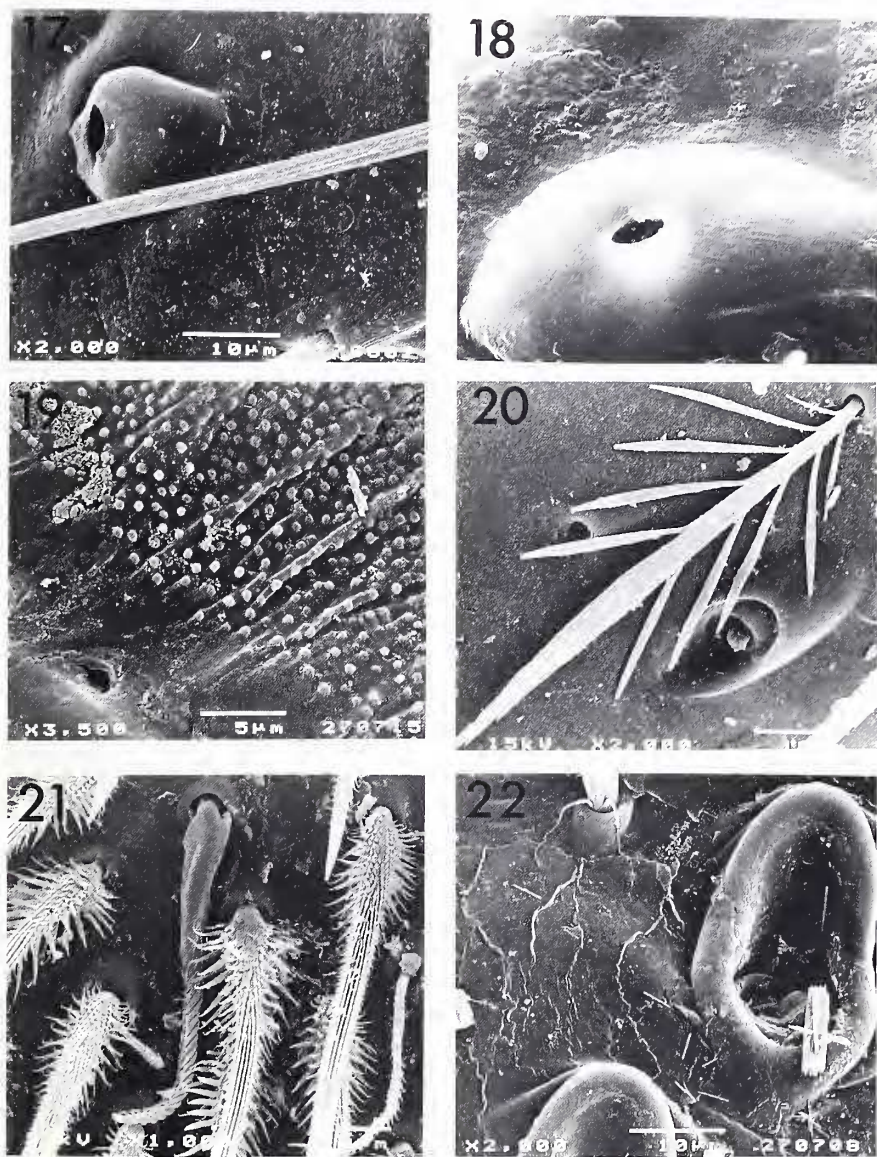
FIGS 5-10

Range of the ridged, plesiomorphic type of leg surface. - 5: *Thaida* sp. from Chile (Thaididae), metatarsal surface; 6: *Encyocrypta* sp. from New Caledonia (Mygalomorpha: Barychelidae), tarsal surface; 7: *Gradungula sorenseni* (Gradungulidae), tarsal surface; 8: *Otiiothops* sp. from Peru (Palpimanidae: Otiiothopinae), surface of tarsus IV with tarsal organ; 9: *Thasyraea* sp. from Australia (Zoridae), tarsal surface; 10: *Miturga agelenina* (Miturgidae), tarsal surface with sensory pit of unknown function.



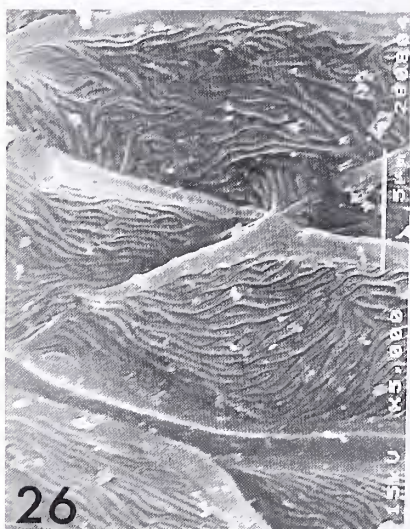
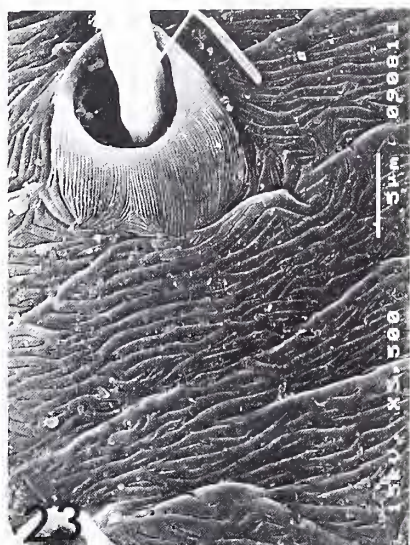
Figs 11-16

Modified types of leg surface. - 11: *Hersilia pectinata* (Hersiliidae), metatarsal surface with anastomosing ridges; 12: *Rhene* sp. from Flores (Salticidae), tarsal surface with tarsal organ, weakly anastomosing type; 13: *Porroptis nitidula* (Thomisidae), metatarsal surface of weakly modified thomisid type; 14: *Xysticus audax* (Thomisidae), papular tibial surface; 15: *Leprolochus* sp. from NE Brazil (Zodariidae), irregularly modified, almost smooth tarsal surface; 16: *Steriphopus* sp. from Indian Himalaya (Palpimanidae), scaly tip of metatarsus close to weakly ridged area.



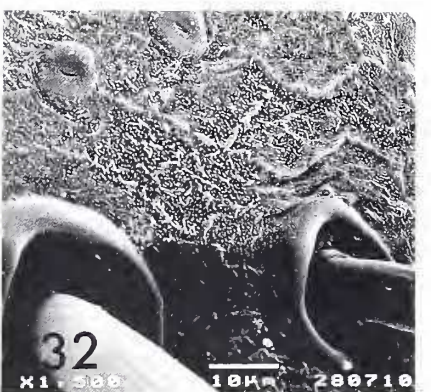
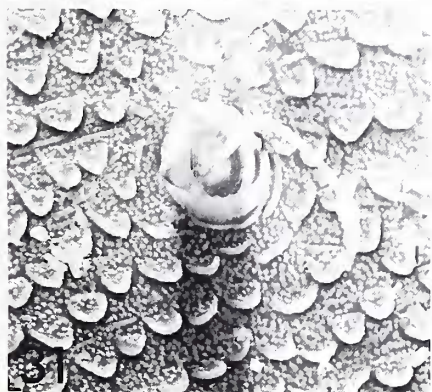
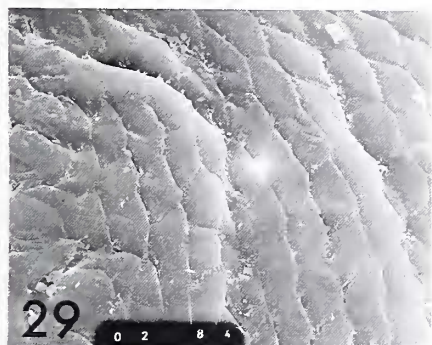
FIGS 17-22

Smooth and modified types of leg surface. - 17: *Nesticella nepaleusis* (Nesticidae), smooth tarsal surface; 18: *Kukulcania hibernialis* (Filistatidae), smooth tarsal surface around tarsal organ; 19: *Zodarion trispinosum* (Zodariidae), femoral base, partly with papular surface; 20: *Creugas gulosus* (Corinnidae: Corinninae), smooth metatarsal surface; 21: *Adonea variegata* (Eresidae), smooth metatarsal surface; 22: *Homalonychus theologus* (Homalonychidae), smooth tarsal surface with irregular "scaly" pattern.



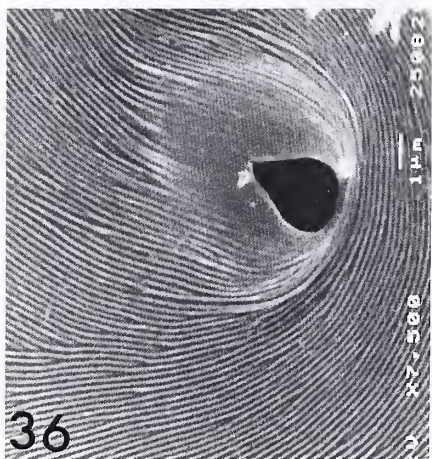
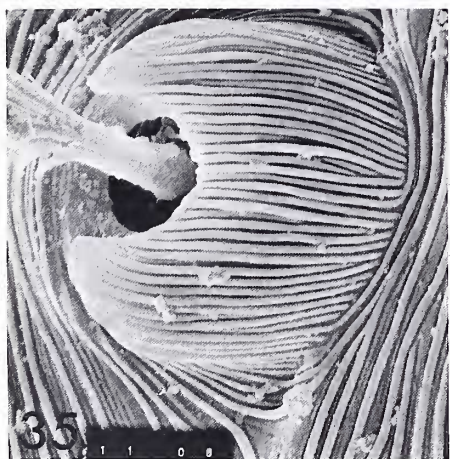
FIGS 23-26

Mixed leg surface patterns. - 23: *Sphingius* sp. from Sri Lanka (Corinnidae: ? subfamily), tarsal surface; 24: *Drymusa silvicola* (Drymusidae), metatarsal surface; 25: *Mecysmauchenius* sp. from Chile (Mecysmaucheniiidae), tarsal surface; 26: N.gen., n.sp. from Vietnam (Caponiidae, new subfamily), metatarsal surface.



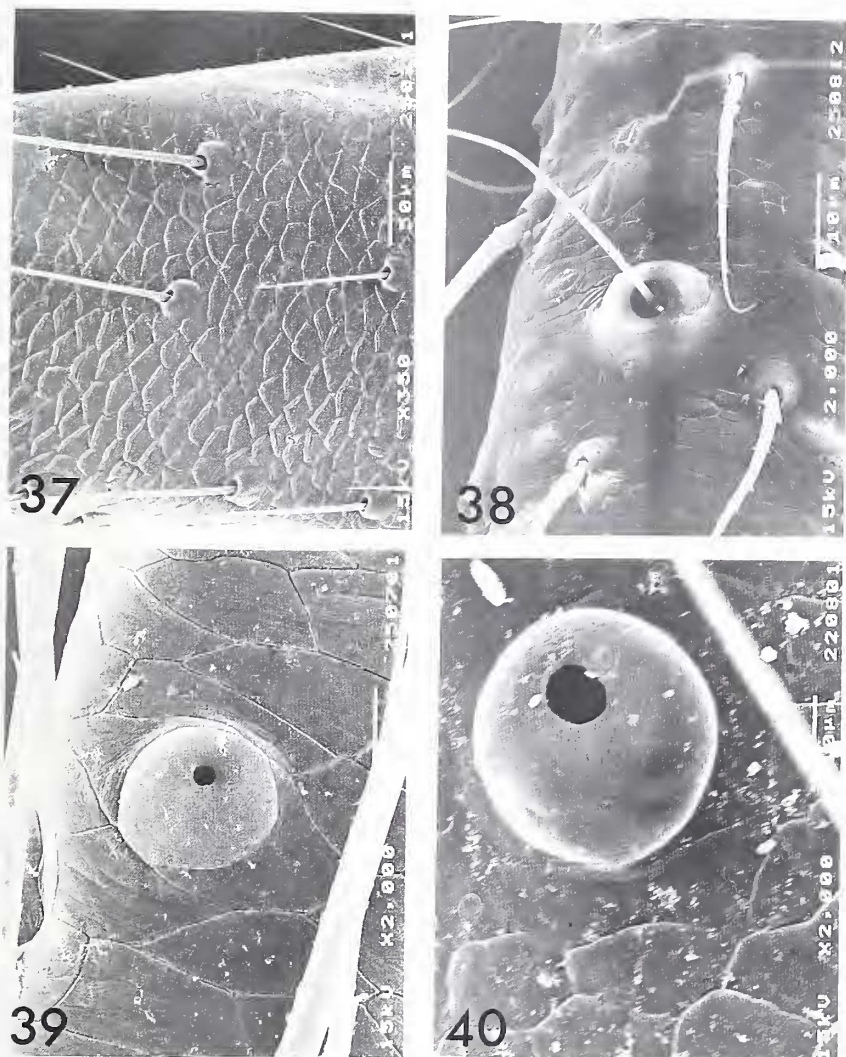
FIGS 27-32

Leg surface in various Arachnid groups. - 27: *Phalangium opilio* (Opilionida: Phalangidae), scaly tarsal surface; 28: *Trombidium* sp. from Finland (Actinotrichida Parasitengona: Trombididae), ridged metatarsal surface; 29: *Ixodes ricinus* (Anactinotrichida Ixodida: Ixodidae), scaly femoral surface; 30: *Stylocellus* sp. from New Caledonia (Opilionida Cyphophthalmi: Stylocellidae), papular metatarsal and scaly tarsal surface; 31: *Liphistiinus malayanus* (Liphistiomorpha: Liphistiidae), metatarsal surface; 32: *Aname pexa* (Mygalomorpha: Nemestiidae), modified tarsal surface of liphistid type.



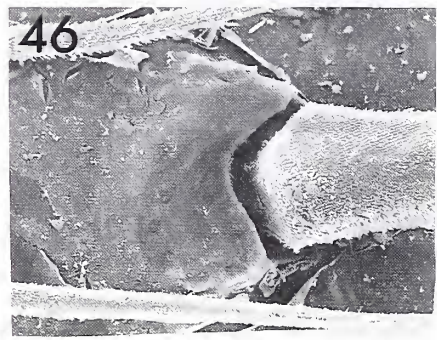
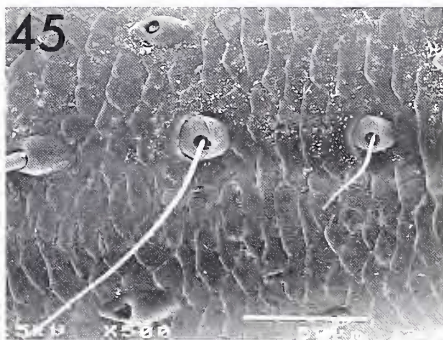
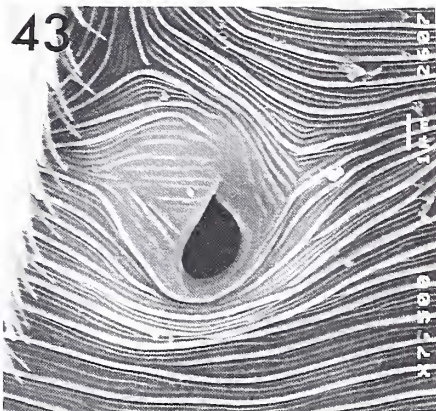
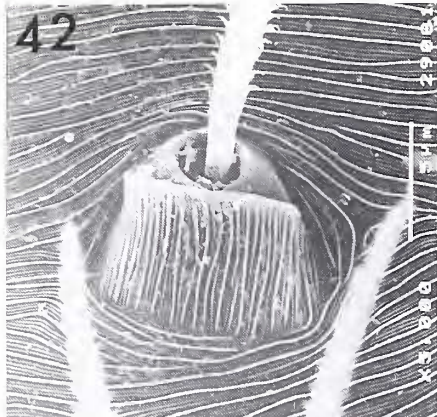
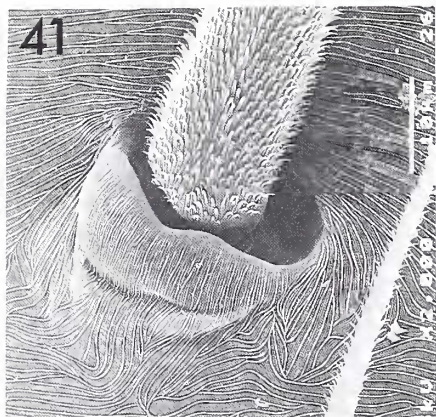
FIGS 33-36

Extension of the plesiomorphic surface pattern to other leg structures. - 33: *Leprolochus* sp. from NE Brazil (Zodariidae), surface of tarsal claws; 34: *Miturga agelenina* (Miturgidae), surface of plumose tarsal hair; 35: *Hahnina pusilla* (Hahniidae), completely ridged metatarsal bothrial base; 36: *Cycloctenus* sp. from New Zealand (Cycloctenidae), completely ridged tarsal organ.



FIGS 37-40

Araneoidean type ultrastructure of doubtful "Palpimanoidea" with cheliceral peg teeth. - 37: *Ero furcata* (Mimetidae), femoral surface; 38: *Micropholcomma* sp. from New South Wales (Micropholcommatidae), theriid type of scaly skin with theriid type of tibial bothrial base; 39: *Ero furcata* (Mimetidae), tarsal surface with tarsal organ; 40: *Araneus diadematus* (Araneidae), tarsal surface with tarsal organ for comparison.



Figs 41-44

Amaurobiomorph ultrastructure of Dinopoidea. Figs. 45-46. Dissimilar ultrastructure of Nico-
damidae and Megadictynidae. - 41: *Tangaroa tahitiensis* (Uloboridae), femoral spine with plu-
mose type of secondary hairs; 42: *Tangaroa tahitiensis* (Uloboridae), ridged bothrial base; 43:
Tangaroa tahitiensis (Uloboridae), non-domed tarsal organ with ridged surface; 44: *Memus
camelus* (Dinopidae), tibial feathery hair with ridged structure extending to the whole stem. -
45: *Nicodamidae* sp. from Tasmania, scaly tibial surface with non-serrate hairs; 46: *Mega-
dictyna thileniisi* (Megadictynidae), smooth metatarsal surface with plumose type of spine.

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